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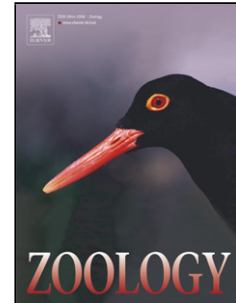
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**Breeding biology of a winter-breeding procellariiform in the
North Atlantic, the Macaronesian shearwater *Puffinus
herminieri baroli***

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Highlights

- Breeding success is strongly related to nest site characteristics.
- Macaronesian shearwaters breed in fairly deep nest cavities and show low inter-annual nest site fidelity.
- Climatic stochasticity events have an effect on foraging and breeding success.

ABSTRACT

The breeding success of burrow-nesting seabirds may be influenced by both nest site characteristics and oceanographic conditions influencing food availability at sea. In this study we describe the breeding biology of the winter-breeding Macaronesian shearwater (*Puffinus lherminieri baroli*), including nest site characteristics and interspecific competition. We also evaluate the possible effects of changing oceanographic conditions on breeding phenology and breeding success. The study was carried out over two breeding seasons on two islands in the North Atlantic Ocean, Cima Islet and Selvagem Grande. Oceanographic characteristics differed between years. On a regional scale, the North Atlantic Oscillation (NAO) index was low and negative in 2011, and on a local scale, birds used areas with significantly lower values of chlorophyll a concentration and significantly higher values of sea surface temperature anomalies. Hatching success was higher in 2012 than in 2011. At both colonies, egg cracking was the main cause of hatching failure, but in 2011 several eggs on Selvagem Grande were deserted. In 2012 birds laid earlier and chicks had longer wings and were heavier. At both colonies, nests that were deeper, were sheltered from prevailing winds and had small chambers and a soil substrate had a higher probability of being used successfully by the birds. Nests occupied solely by Macaronesian shearwaters were much deeper and had less volume than nests shared with other species. Our study suggests that the breeding success of Macaronesian shearwaters is strongly related to nest site characteristics and that at-sea environmental conditions exert a strong influence on reproductive parameters, with birds breeding in a poor year (evaluated in terms of lower marine productivity) laying much later and their chicks growing at a slower rate than in a good year. The influence of nest site characteristics and environmental conditions may

be very important for understanding the breeding ecology of Procellariiformes and may help explain the negative population trend of Macaronesian shearwaters.

Keywords: Procellariiformes; Breeding biology; Nest site characteristics; Nest site fidelity; Oceanographic conditions

1. Introduction

In central-place foraging species that exhibit a protracted breeding season such as seabirds (Orlans and Pearson, 1979), parents need to select and defend suitable nest sites to protect their eggs and chicks and must optimise prey delivery to chicks in order to breed successfully (Drummond and Leonard, 2010). Breeding success of burrow-nesting Procellariiformes (e.g., albatrosses, petrels and shearwaters) may be influenced by both nest site characteristics and oceanographic conditions that influence food availability at sea.

Annual or medium-term variations in sea surface temperature (SST) and chlorophyll *a* (Chl *a*) concentration have been linked to fluctuations in the distribution and reproductive success of seabirds (e.g., Durant et al., 2003; Quillfeldt et al., 2007; Paiva et al., 2013a; Berlincourt and Arnould, 2015) and have generally been analysed in the context of large-scale (spatial and temporal) atmospheric processes such as the El Niño Southern Oscillation (ENSO) in the Pacific Ocean, or the North Atlantic Oscillation (NAO) in the North Atlantic Ocean (e.g., Ramos et al., 2002; Durant et al., 2003; Sandvik et al., 2005). Increasing SST and subsequent higher SST anomalies (SSTa) may block nutrient-rich up-welling zones that can influence primary productivity and impact seabird breeding success through changes in prey availability (Ramos et al., 2002; Peck et al., 2004; Quillfeldt et al., 2007).

Nest site selection can be driven by a combination of physical and social features, including nest microclimate, level of disturbance from conspecifics, distance and density of individuals from different species and predation risk (Ramos et al., 1997; Mallory and Forbes, 2011). The characteristics of the nest sites of burrow-nesting Procellariiformes may also influence their reproductive success (Ramos et al., 1997), particularly for winter-breeding species, when adverse meteorological conditions, such as strong rainfall, could increase the importance of burrow characteristics for breeding success (Thompson and Furness, 1991). In fact, Ramos et al. (1997) showed that nest

cavities of winter-breeding Procellariiformes appear to be more concealed than nest cavities of summer-breeding species, but this aspect has received very little attention. In the Pacific Ocean, Bester et al. (2007) observed that egg and chick mortality of the providence petrel (*Pterodroma solandri*), a tropical burrow-nesting procellariiform breeding during the winter on Lord Howe Island, Australia, were strongly correlated with the distance between the nest chamber and the burrow entrance, with more losses occurring in nests whose chamber was closer to the nest entrance. McClelland et al. (2008) observed that egg abandonment and breeding success of Tristram's storm petrel (*Oceanodroma tristrami*) on Laysan Island and French Frigate Shoals, Northwest Hawaiian Islands, were affected by rainfall and competition with larger burrowing seabirds for nest sites.

In the North Atlantic, global positioning system (GPS) and global location sensing (GLS) tracking devices have been widely used to describe the foraging distribution of summer-breeding seabirds such as Cory's shearwater (*Calonectris borealis*; Haug et al., 2015; Missaglia et al., 2015) or Desertas petrel (*Pterodroma deserta*; Ramírez et al., 2016). Recently, GLS devices were also used to evaluate the at-sea distribution of the winter-breeding Macaronesian shearwater *Puffinus lherminieri baroli* (Neves et al., 2012; Ramos et al., 2015, Paiva et al., 2016). In the North Atlantic, the breeding biology of summer-breeding species such as Cory's shearwater (Ramos et al., 2003 and references therein) has also been well studied, yet there is little information regarding the breeding biology of winter-breeding species such as the Macaronesian shearwater. Monteiro et al. (1996a) provided information about breeding phenology and egg dimensions, and Ramos et al. (1997) described the nest site characteristics of several procellariiform species breeding in the Azores archipelago, including the Macaronesian shearwater. An important finding of these previous studies is the existence of interspecific competition for nesting burrows, with excavation and occupation of nests of smaller species, including the Macaronesian shearwater, by the much larger Cory's shearwater. However, the possible effect of nest site characteristics on the breeding success of winter-breeding Procellariiformes has not been examined.

The Macaronesian shearwater is endemic to the Macaronesian Islands, North Atlantic Ocean. Recent revision of the taxonomy of the *Puffinus assimilis*/*P. lherminieri* complex led BirdLife International (2014) to suggest that *P. baroli* breeding on the Azores, Madeira, Selvagens and Canaries and *P. boydi* on the Cape Verde islands should be regarded as subspecies of *P. lherminieri*. Macaronesian shearwater is

considered rare by BirdLife International and is a species of conservation concern in Europe (BirdLife International, 2004). According to the European Red List of Birds (BirdLife International, 2015) the population size is estimated to be decreasing at a rate approaching 10% in 67 years. As this species has a small, apparently decreasing population, it is presently classified as near threatened (BirdLife International, 2015). Selvagem Grande holds the largest population of the species, with 2050 to 4900 breeding pairs (Oliveira and Moniz, 1995), but recent trends are unknown. Considering the recent population decline on Tenerife, Canary Islands (Rodríguez et al., 2012), information on the breeding biology of Macaronesian shearwater at other important localities in the North Atlantic is crucial to identify conservation issues at breeding colonies, as the factors influencing breeding success are often site-specific (Warham, 1990; Ramos and del Nevo, 1995). A burrow-nesting procellariiform, the Macaronesian shearwater is expected to show strong nest site fidelity (Warham, 1990; Bried et al., 2003), but data are needed to evaluate this assumption. This species may also be affected by annual changes in oceanographic conditions (e.g., SST and Chl a), leading to strong variations in diet and feeding ecology (Ramos et al., 2015), but no information is available concerning how such annual changes might affect the breeding success of Macaronesian shearwaters.

Food availability (determined by oceanographic and climatic features; Ramos et al., 2015) and nest site characteristics (Ramos et al., 1997) are likely to be the two most significant determinants of reproductive performance in burrow-nesting Procellariiformes, but most studies have not examined these two aspects in conjunction. Nest site characteristics are of great importance in terms of conservation because providing appropriate artificial nest sites can improve the breeding success and consequently the conservation status of threatened seabird species (Bolton et al., 2004; Bourgeois et al., 2015), whereas other threats such as climatic variations impacting food availability are often much more difficult to target. In the present study we describe the breeding biology, including a detailed examination of nest site characteristics, of the winter-breeding Macaronesian shearwater on two islands, Cima Islet and Selvagem Grande, in the Madeira and Selvagens archipelagos, respectively, for two consecutive breeding seasons (2010–2011 and 2011–2012). Our specific objectives were to determine: (i) annual and inter-island variation in reproductive success, (ii) the influence of interspecific competition for nest sites and of environmental factors on hatching

success for each population, and (iii) the possible effects of changing oceanographic conditions on the breeding phenology and breeding success of each population.

1. Materials and methods

2.1. Study sites

Field work concerning breeding phenology, breeding success and nest characteristics on Cima Islet (CI) and Selvagem Grande (SG) (Fig. 1) was carried out during the breeding seasons of 2010–2011 and 2011–2012 (2011 and 2012 hereafter). Nest site fidelity was studied between 2010 and 2013.

Cima Islet (33°01'N 16°22'W) is a 32-ha rocky islet located south-east of Porto Santo Island, 50 km north-east of Madeira Island. It holds small populations of Macaronesian shearwaters, Cory's shearwaters, Bulwer's petrels (*Bulweria bulwerii*), and band-rumped storm petrels (*Hydrobates castro*). Selvagem Grande (30°09'N, 15°52'W; 245 ha) is located ~296 km south of Madeira Island. Besides Macaronesian shearwaters, the island has the world's largest colony of Cory's shearwaters (~30,000 breeding pairs; Granadeiro et al., 2006) and large populations of Bulwer's petrels, white-faced storm petrels (*Pelagodroma marina*) and band-rumped storm petrels.

2.2. At-sea distribution and environmental variability

In 2010 and 2011, 10 GLS devices (MK18L; British Antarctic Survey, Cambridge, UK) were deployed each year on incubating Macaronesian shearwaters, and 13 were recovered between February and April of the following years (2011: 3 on CI and 4 on SG; 2012: 4 on CI and 2 on SG). Tracking devices were attached with a cable tie to numeric metal rings and represented ~1% of bird body mass.

The GLS devices enable the calculation of the position (twice per day) from ambient light level readings with reference to time. Latitude and longitude were estimated from day (night) length and the time of local mid-day (mid-night), respectively, in relation to Greenwich Meridian Time (Phillips et al., 2004). Full details of the GLS analyses are presented by Ramos et al. (2015).

Two environmental predictors were selected to characterise the marine areas of the North Atlantic used by Macaronesian shearwaters on a local scale (inside the 50% kernel utilisation distribution of birds), including SSTa computed from SST data and Chl a concentration (see Ramos et al., 2015 for analysis description and more details). To describe environmental conditions in the North Atlantic, we used the NAO index,

which is characterised by an oscillation in atmospheric mass between the subtropical high-pressure zone of the Azores and the low-pressure zone of Iceland (Ottersen et al., 2001). The extended winter (December–March) NAO index from Hurrell (1995) (http://gcmd.nasa.gov/records/GCMD_NCAR_NAO.html) was used in this study. During the positive phase of the winter NAO index, westerly winds strengthen and move northwards, leading to an increase in precipitation and sea surface temperatures in northern Europe and the opposite conditions in southern Europe (Ottersen et al., 2001; Stenseth et al., 2003). Recent studies suggest that environmental stochasticity (depicted by NAO index values) results in an unusual decrease in ocean productivity regimes (Frederiksen et al., 2004). This has been linked with reductions in prey abundance and availability for North Atlantic summer-breeding seabirds (Paiva et al., 2013a). Values of the environmental predictors (Chl a and SSTa) from inside the 50% kernel utilisation distribution (likely to represent the main foraging area; Paiva et al., 2013a) were extracted within R with the *extract* function from the *raster* package (Hijmans and van Etten, 2014).

2.3. Breeding parameters

Surveys to locate nest sites were conducted on Selvagem Grande from 5 February to 6 March 2010, 10 March to 2 May 2011, 24 February to 21 May 2012, and 27 February to 24 March 2013. Fieldwork on Cima Islet started in 2011. Two visits occurred during that year, the first one from 6 to 10 April and the second one on 15 May. This islet was visited three times in 2012 (20–24 February, 15–20 March, and 13–17 May), and once in 2013 (9–13 February). At both colonies nest searches were conducted every night along cliff areas with suitable breeding habitats, by inspecting all burrows and rock crevices whenever we heard Macaronesian shearwater vocalisations. These areas were characterised by the presence of many small to moderate-size rocks (10–100 cm long) buried in the soil, which formed the walls and/or roofs of natural nesting cavities occupied by Macaronesian shearwaters. Each year all nests with an egg were marked with a number painted on a small stone beside the nest entrance. Adults were captured by hand in their nests and ringed with an individually numbered metal ring. Body mass (g), tarsus length (mm), and wing length (maximum flattened and straightened wing chord, mm) were measured for each individual. A blood sample (~150 µl) was taken from each bird's brachial vein (CI: $n = 67$; SG: $n = 80$) for molecular sexing following the methods by Fridolfsson and Ellegren (1999) after DNA had been extracted using an

adaptation of the Chelex method (Walsh et al., 1991). Egg length and width ($n = 57$; CI: $n = 19$; SG: $n = 38$) were measured with calipers (± 0.1 mm).

Bird ringing, biometrics and blood sampling did not take more than 10 min and on no occasion did it interfere with reproduction or had visible deleterious effects on study animals. All procedures complied with the Portuguese requirements and regulations of animal care. All fieldwork was approved and certified by annual permits by the relevant authorities, the Service of Madeira Natural Park.

During the breeding seasons of 2011 and 2012, nests were checked daily (2011: 13 nests on CI, 15 nests on SG; 2012: 10 nests on CI, 26 nests on SG). Hatching dates were obtained in the field, based on daily visits, or estimated from chick wing length using mean values of chicks of known age. The visit made on 15 May 2011 to Cima Islet was important to determine hatching success and check whether the chicks found during the first visit had successfully fledged (chicks older than 30 days were assumed to have fledged successfully).

2.4. Nesting burrow characteristics

Data were collected from 88 burrows (26 on CI, 62 on SG) located along cliff areas. During the visits to each colony, all nests with adult birds, but without eggs, were checked once a week to determine if females had eventually laid eggs. For each burrow, we used a retractable aluminium tape to measure: entrance depth, chamber depth, chamber height, and chamber width. Total depth was the maximum distance from the entrance of the nest to the deepest point of the chamber (following the line of the entry corridor) and was subdivided into entrance depth (the longest measurement of the entrance corridor, i.e. until it enlarged into a chamber) and chamber depth (the remaining straight line to the deepest point of the chamber). Chamber height was the maximum length of the nest chamber perpendicular to the ground. Chamber width was the maximum length of the chamber perpendicular to the depth of the chamber and parallel to the ground. To characterise nest sites, the variables used were total nest depth (entrance depth + chamber depth), chamber depth, chamber volume in cm^3 (chamber depth \times chamber height \times chamber width), substrate of nest chamber (soil, rock, or mixture), and nest entrance orientation (north, east, south or west).

2.5. Nest site fidelity and occupation of nests by other seabird species

Each year, all occupied nests were monitored to determine if breeding birds retained the same nest and mate. Because all handled birds were ringed, we were able to determine if nests were used by a breeding pair from the previous year(s) or by a different pair. For this analysis, only birds found at a nest for at least two years were considered (CI: $n = 11$; SG: $n = 33$). This information was collected for three breeding seasons (2011–2013) for Cima Islet and for four seasons for Selvagem Grande (2010–2013). All Macaronesian shearwater nests occupied by other seabird species were also noted (CI: $n = 10$; SG: $n = 14$).

2.6. Chick growth on Selvagem Grande

We monitored the growth of four chicks (1–30 days old) in 2011 and 13 chicks in 2012 (10–60 days old). The sample size in 2011 was small, but should reflect the environmental conditions of this year because these were the only chicks that survived. In both years, nests were visited daily at the same time (around 17:00 h) to measure the wing length (± 1 mm) and mass (± 2 g) of each chick.

2.7. Statistical analyses

Generalised linear mixed models (GLMMs) were used to test the year effect on Chl a and SSTa at GLS locations within the 50% kernel utilisation distribution, with individual as a random effect because several individuals were tracked for more than one year. The effects of sex, breeding colony, and their interaction on adult bird biometrics were tested using a factorial ANOVA. Egg volume index was calculated using the formula: $(\text{length} \times \text{breadth}^2)/1000$ (Coulson, 1963) and compared between colonies with one-way ANOVA (egg volume did not differ between years). The influence of nest site characteristics (nest_char) on laying propensity (lay_succ; 1 = with egg, 0 = without egg), hatching success (1 = hatched, 0 = not hatched), and burrow exclusivity (1 = only Macaronesian shearwaters, 0 = also used by other seabird species for nesting or roosting) was tested with generalised linear models with binomial distribution, fitting the influence of (i) nest total depth (entrance depth + chamber depth) = total_depth, (ii) chamber depth = chamber_prof, (iii) chamber volume (depth \times height \times width) = chamber_vol, (iv) substrate (soil, mixture, or rock), and (v) nest entrance orientation (north, east, south or west) = orientation, according to the formula: $\text{fit} = \text{glm}(\text{lay_succ} \sim \text{total_depth} + \text{chambre_vol} + \text{chamber_prof} + \text{substrate} + \text{orientation}, \text{data} = \text{nest_char}, \text{family} = \text{binomial}(\text{link} = \text{"logit"}))$. The odds ratio was calculated as \exp

(coef (mylogit)). The effects of (i) year and island and (ii) egg volume and female weight on hatching success (1 = hatched, 0 = not hatched) were analysed with GLMs, with binomial error distribution and logit link function. The effect of year, island, and their interaction on chick hatching date (number of days since 1 January, log-transformed) was analysed with a factorial ANOVA. To compare chick growth curves between 2011 and 2012 for Selvagem Grande, mean wing length and body mass were plotted against chick age.

All statistical analyses were performed using the software R (R Core Team, 2014). Computations were carried out using several functions within different R packages (e.g., *MASS*, *adehabitatHR*, and *raster*) and some custom-built functions. GLMMs were run using functions within the R packages *lme4* (Bates et al., 2011) and *LmerTest* (Kuznetsova et al., 2013). Means are given \pm SD and all P -values < 0.05 were considered significant.

2. Results

3.1. Foraging areas and oceanic conditions

During the breeding period, the Macaronesian shearwaters from both islands foraged in the Canary Current area, although birds from Cima Islet also foraged more offshore to the north, west into the Azores region, and in the Portuguese Current area (Fig. 1). Oceanographic characteristics differed between 2011 and 2012. On a regional scale, the extended winter NAO index was low and negative in 2011 (-1.57) and positive in 2012 (3.17). On a local scale, birds from both islands used areas with significantly lower values of Chl a in 2011 than in 2012 (CI: 0.8 ± 0.1 vs. 1.2 ± 0.3 mg m⁻³; SG: 1.2 ± 0.2 vs. 1.6 ± 0.8 mg m⁻³; GLMM: $F_{1,329} = 15.14$, $P < 0.001$ and $F_{1,845} = 3.01$, $P = 0.06$, respectively), and significantly higher values of SSTa in 2011 than in 2012 (CI: 0.6 ± 0.4 vs. -1.1 ± 0.4 °C; SG: 0.7 ± 0.2 vs. -0.6 ± 0.7 °C; GLMM: $F_{1,329} = 17.98$, $P < 0.001$ and $F_{1,845} = 19.33$, $P < 0.001$, respectively).

3.2. Hatching dates and breeding success

The birds from Cima Islet were larger and heavier than those from Selvagem Grande. We found significant differences in wing length (CI = 182.63 mm, SG = 181.12 mm; $F_{1,137} = 5.1$, $P = 0.02$), tarsus length (CI = 37.28 mm, SG = 36.68 mm; $F_{1,137} = 16.4$, $P < 0.001$), and body mass (CI = 169.29 g, SG = 163.46 g; $F_{1,143} = 4.9$, $P = 0.03$) between the two islands, but no difference between sexes and no interaction between sex and

island (two-way ANOVA, wing: $P = 0.35$, tarsus: $P = 0.87$, and body mass: $P = 0.42$). Similarly, the eggs from Cima Islet were longer (CI = 49.39 mm, SG = 47.84 mm; $F_{1,55} = 8.8$, $P = 0.004$), wider (CI = 34.65 mm, SG = 33.60 mm; $F_{1,55} = 10.1$, $P = 0.002$), and had a greater volume (CI = 59.37 cm³, SG = 54.13 cm³; $F_{1,55} = 16.0$, $P < 0.001$) than those from Selvagem Grande.

Hatching dates differed between islands ($F_{1,32} = 4.6$, $P = 0.04$), but chicks hatched earlier in 2012 than in 2011 ($F_{1,32} = 91.2$, $P < 0.001$) on both islands. Mean hatching dates in 2011 were 10 April \pm 2.2 days on CI and 2 April \pm 1 day on SG. In 2012, mean hatching dates were 17 March \pm 3.7 days on CI and 16 March \pm 6.9 days on SG.

Hatching success was significantly higher in 2012 than in 2011 (Wald $\chi^2 = 4.6$, $P = 0.03$). Hatching success on Cima Islet tended to be higher than on Selvagem Grande, although the difference did not reach significance (Wald $\chi^2 = 3.6$, $P = 0.06$). However, there was no interaction between year and island (Wald $\chi^2 = 0.1$, $P = 0.78$). Fledging success was similar between years and islands (Table 1). We did not find significant differences in volume between the eggs that hatched and those that did not hatch (hatched: 56.6 ± 4.8 cm³, $n = 13$ vs. not hatched: 55.4 ± 3.3 cm³, $n = 17$; Wald $\chi^2 = 0.22$, $P = 0.82$), or female body mass between birds whose eggs hatched (174.7 ± 13.1 g, $n = 13$), and those whose eggs did not hatch (166.6 ± 12.7 g, $n = 17$; Wald $\chi^2 = 1.38$, $P = 0.17$).

For both colonies, egg cracking was the main cause of hatching failure. However, on Selvagem Grande seven eggs (i.e., 46.7%) were deserted in 2011, and in 2012, four eggs (i.e., 15.4%) were washed away with the rain that entered nest burrows during a heavy rainstorm. This storm was also responsible for the death of two chicks caused by nest flooding (Table 1).

3.3. Nest site characteristics

At both colonies, laying probability increased with nest cavity depth (corridor + chamber) and when nest entrances were oriented south or west. As nest depth increased, laying became 4.87 times more likely on Cima Islet and 1.43 times more likely on Selvagem Grande. On Cima Islet, laying probability decreased as nest chamber volume increased, whereas on Selvagem Grande it decreased when nest chamber substrates were rocky or mixed. On Selvagem Grande, hatching success increased 2.65 times as

nest depth increased. At both colonies, hatching probability decreased in nests with larger chambers and rocky substrates (Table 2).

Nests occupied only by Macaronesian shearwaters were significantly deeper (only MS: 82.1 ± 7.0 cm vs. shared: 52.6 ± 9.0 cm; $Z = 3.7$, $P < 0.05$) and had a significantly smaller chamber volume (only MS: 3115.1 ± 711.2 cm³ vs. shared: 7912.0 ± 801.6 cm³; $Z = 2.3$, $P < 0.05$) than those shared with other Procellariiformes.

3.4. Nest site fidelity and occupation of nests by other seabird species

At both colonies, birds showed low nest site fidelity. Only 9% of the birds breeding on Cima Islet and 18% on Selvagem Grande used the same nest for three successive years. Of the 8 successful birds on Cima Islet (3 in 2011 and 5 in 2012), 6 bred in the same burrow the following year, and similar figures were obtained for Selvagem Grande, with 12 of 14 successful birds (3 in 2011 and 11 in 2012) returning to breed in the same nest the next year.

Several nests of Macaronesian shearwaters were occupied by other species. Most nests were occupied by Bulwer's petrels and Cory's shearwaters. Occupation of nests by band-rumped storm petrels was only observed on Cima Islet (Table 3). Despite the differences in the breeding periods among these four species (Bulwer's petrel: April–September; Cory's shearwater: February–October; band-rumped storm petrel: September–February; Macaronesian shearwater: December–May) we observed that in 2011 Bulwer's petrels on Selvagem Grande arrived in late March when Macaronesian shearwaters were still incubating, and we found cracked eggs after their arrival. In 2012 Bulwer's petrels arrived in the middle of April, when Macaronesian shearwater chicks were almost one month old. At both colonies we observed a Macaronesian shearwater and a Bulwer's petrel together in the same nest. The period of colony attendance by band-rumped storm petrels shows a large overlap with that of Macaronesian shearwaters and although the former species does not weigh more than ca. 30% of a Macaronesian shearwater, we observed that when a nest was occupied by band-rumped storm petrels, Macaronesian shearwaters did not occupy this nest.

3.5. Chick growth on Selvagem Grande

Chicks had longer wings and were heavier in 2012 than in 2011. On average, 20-day old chicks weighed 24.3 g less, and their wings were 10.2 mm shorter, with both measures exhibiting much longer error bars in 2011 than in 2012 (Fig. 2A and B). In 2012, body

mass was monitored until fledging, and growth rates were higher until 40 days post-hatching, followed by stabilization until 50 days (when chick body mass peaked at 182.6 ± 25.5 g), and by a slight decrease before fledging from 57 to 61 days post-hatching (Fig. 2A). Wing growth rate was low for chicks under ~20-day old, and then increased as the primaries emerged (Fig. 2B).

3. Discussion

Our results suggest that breeding success of Macaronesian shearwaters was strongly related to nest site characteristics. At both colonies, nests that were deeper, sheltered from the prevailing winds, with small chambers and a soil substrate had a much higher probability of being used successfully. Our data also show that environmental conditions at sea exerted a strong influence on reproductive parameters, with birds breeding in a poor year (evaluated in terms of lower marine productivity) laying much later and their chicks growing at a slower pace than in a good year. Therefore, the influence of nest site characteristics and environmental conditions may be very important for understanding the breeding ecology of Procellariiformes, and particularly of winter-breeding species such as the Macaronesian shearwater.

4.1. Breeding success and nest site characteristics

Macaronesian shearwaters breeding on Cima Islet were intermediate in size between those on Selvagem Grande and those from the Azores (Monteiro et al., 1996b). Larger body size of Macaronesian shearwaters at higher latitudes probably results from a combination of factors such as geographic range, climatic conditions, and the availability and quality of resources, similarly to what occurs in other seabird species such as the wedge-tailed shearwater (*Ardenna pacifica*; Asmussen, 2006; Bull, 2006) and Cory's shearwater (Gómez-Díaz et al., 2006). No significant interaction was found between sex and island, indicating that no geographical variation in the extent of sexual size dimorphism occurs. Meathrel et al. (1993) found that the reproductive success of short-tailed shearwaters (*Ardenna tenuirostris*) is independent of egg size, and likewise we did not find a relationship between hatching success and the size of either the female or the egg.

Our results show that Macaronesian shearwaters breed in fairly deep nest cavities but nest site characteristics differed between islands, most likely due to variation in the availability of nest cavities between the two islands. Nests on Cima Islet were deeper

than those on Selvagem Grande. Deep nests are likely to be safer for eggs and chicks given their greater protection from possible flooding, predation (e.g., from yellow-legged gulls; Bester et al., 2007) and disturbance from other shearwater species (Ramos et al., 1997; this study). Spring breeding species, such as the Yelkouan shearwater (*Puffinus yelkouan*) breeding on the Hyères archipelago, France, also select cavities that provide a high degree of concealment and protection from predators and inclement weather, occupying the deepest cavities preferably with a winding tunnel and a slab or branch protecting the entrance (Bourgeois et al., 2014). In the Azores, summer-breeding species such as Cory's shearwater and Bulwer's petrel also nest in sheltered nest site cavities, ranging from relatively open nest sites to very deep burrows (Ramos et al., 1997).

We also found a relationship between nest characteristics and hatching success. Laying probability increased with nest depth and when the nest entrance was oriented southwards or westwards, suggesting that acquiring a nest sheltered from the prevailing winds and rain (at both colonies, the prevailing winds and harshest weather conditions come from the northeast; Young, 1999; Santos and Aguiar, 2006) increases the chances of breeding successfully. On Rhum Island, Scotland, Thompson and Furness (1991) also found a selective advantage for pairs of Manx shearwater (*Puffinus puffinus*) choosing high quality (dry) burrows. The egg and chick mortality of the Providence petrels (*Pterodroma solandri*) breeding on Lord Howe Island, Australia, during the austral winter is mainly determined by burrow inundation and is strongly correlated with the distance between the burrow entrance and the nest chamber (Bester et al., 2007). In the Azores archipelago Ramos et al. (1997) found that the nests of summer-breeding Procellariiformes had their entrances oriented to all compass directions.

The size of the chamber and the type of substrate were also important because, at both colonies, the probability of hatching decreased for nests with larger chambers and when the nest substrate was rocky. Similar results were obtained by Ramos et al. (1997) for summer-breeding Cory's shearwater in the Azores. Larger chambers allow the entry of larger seabird species such as Cory's shearwater, which consequently causes the cracking of Macaronesian shearwater eggs. Also, eggs are more likely to tumble or to break on a rocky substrate than on a soft ground.

Clearly, the nests occupied solely by Macaronesian shearwaters were much deeper and had less volume than the nests shared with Cory's shearwaters, Bulwer's petrels, and

Band-rumped Storm petrels, highlighting the importance of high-quality nesting burrows to avoid detrimental interspecific competition.

4.2. Environmental factors influencing breeding parameters

High colony fidelity is generally accepted for long-lived Procellariiformes (Warham, 1990), but we found low inter-annual nest site fidelity in Macaronesian shearwater. This might result from low breeding success, predation or a tendency of birds to change mate and nest after a failure (e.g., Bradley et al., 1990; Thompson and Furness, 1991; Mougin et al., 2000). Competition for a limited number of nest sites may also have been a factor with some Macaronesian shearwater nests seen to be occupied by other species. Our results could also be influenced by the fact that some individuals may not breed every year (e.g., when food availability is low). Poor food availability would be expected to reduce the number of pairs commencing a breeding attempt (Dunlop et al., 2002), and it is likely that non-breeding is a common response to sub-optimal environmental conditions during the pre-laying period (Dunlop et al., 2002). Mougin (1996) also detected a relatively low nest site and mate fidelity for Bulwer's petrel on Selvagem Grande, which suggests that fidelity might depend on the stability of the nesting habitat. Another possibility is that birds did not use the same nests each year but an adjacent one.

We found that hatching dates differed between years but were similar between colonies during a given year. At both colonies, chicks hatched between mid-March (16/17 March) and early April (2/10 April) and the hatching period lasted up to 14 days. Considering that incubation lasts 48 days (Oliveira and Moniz, 1995), egg laying should have begun at the end of January. Therefore, our estimates concerning the laying period are in general agreement with those reported for Selvagem Grande (Oliveira and Moniz, 1995) and for the birds breeding in the Azores Archipelago (Monteiro et al., 1996a).

The delayed laying season, greater number of deserted eggs, lower hatching success, chicks' lighter body mass and shorter wings in 2011 compared to 2012 could be related to inter-annual fluctuations in food supply, given the poor oceanographic conditions in 2011, and may have been a consequence of changes in water mass driven by climate and stochastic variation in prey abundance and availability (Neves et al., 2012; Paiva et al., 2013a; Ramos et al., 2015). Availability of food to seabird populations is difficult to measure but is clearly influenced by oceanic conditions within the foraging range of the individuals (e.g., Abrams and Underhill, 1986; Ballance, 2007; Elliott et al., 2008).

Similarly, Asmussen (2006) reported that during less favourable years (El Niño years) the eggs of little shearwaters (*Puffinus assimilis tunneyi*) in Western Australia hatched later and less synchronously, and chick provisioning rates were lower and relatively erratic.

The positive values of SSTa, low Chl a, and low values of the NAO index observed in 2011 may have resulted in lower marine productivity and prey abundance in the North Atlantic (Paiva et al., 2013a; Ramos et al., 2015). In this area, years with a lower NAO index like in 2010/2011 are associated with an unusually strong upwelling along the Portuguese and African coasts. This phenomenon drives fish larvae and plankton offshore and causes their mortality (Santos et al., 2004, 2007), resulting in low recruitment of small pelagic prey for seabirds (Santos et al., 2004; Paiva et al., 2013a). For instance, Cory's shearwaters breeding on Berlenga Island (off the Portuguese coast) enlarged their foraging range significantly and had lower hatching success in 2011 than between 2007 and 2010 (Paiva et al., 2013b). This is likely indicative of the lower marine productivity in the area surrounding their breeding colony in 2011. Because Macaronesian shearwaters concentrate their foraging effort in the neritic Portuguese and African waters during the breeding period, similar stochastic climatic events and the associated fluctuations in prey availability probably had an effect on the foraging and breeding success of the Macaronesian shearwater populations from the Madeira and Selvagens archipelagos (Ramos et al., 2015). Although our chick sample size for 2011 was small, the lower mean and much larger coefficient of variation in body mass for 2011 than 2012 support the idea that oceanic conditions were poorer in 2011 (Ramos et al., 2015). Therefore, and as shown in other species (Takahashi et al., 1999; Asmussen, 2006; Berlincourt and Arnould, 2015), adult Macaronesian shearwaters may struggle to meet their own energetic requirements plus those of their chicks during the years when oceanic conditions are less favourable. As current oceanographic conditions appear to be an important influence on the breeding biology of these and other seabird species in this region, it is important to conduct a more extensive assessment of these factors to accurately determine those which negatively affect prey availability and foraging activity.

4.3. Conservation considerations

Overall, our study suggests that oceanographic variables and nest site characteristics are crucial for understanding the drivers of annual changes in breeding parameters of

winter-breeding burrowing Procellariiformes such as the Macaronesian shearwater. Even in a good year, extreme weather events, such as the rainstorm which occurred in 2012, may play an important role in explaining the breeding success of these species (Bester et al., 2007; this study). Given the current negative population trends of many small procellariiform species worldwide (Day et al., 2003; Le Corre et al., 2003; Rodríguez et al., 2012), those that breed in wet regions and during the winter are more at risk from inclement weather and competition for adequate nest sites with other procellariiform species (Ramos et al., 1997; this study). Although the effects of increasingly poor conditions at sea due to climate change (Doney et al., 2012) are difficult to minimise, the conservation of decreasing populations may be boosted by the installation of appropriate artificial nests (Bolton et al., 2004; Bourgeois et al., 2015).

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Figure legends

Fig. 1. Marine areas exploited by birds from Cima Islet and Selvagem Grande during the breeding seasons (December–May) of 2010–2011 (Cima Islet: $n = 3$, Selvagem Grande: $n = 4$) and 2011–2012 (Cima Islet: $n = 4$, Selvagem Grande: $n = 2$). Data presented are the 95% (dashed line) and 50% (continuous line) kernel utilisation distribution derived from global location sensing (GLS) loggers, after Ramos et al. (2015). Bathymetry shown in the background with colonies marked with white stars.

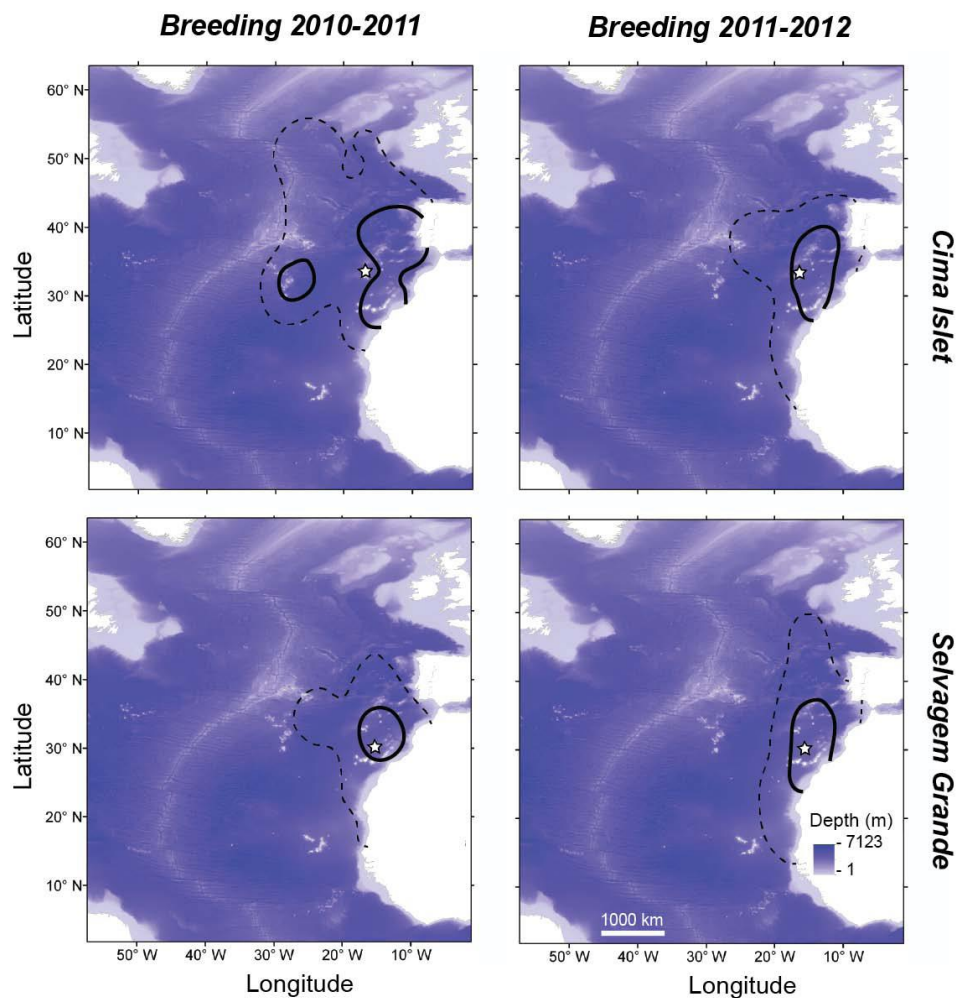


Fig. 2. Growth curves for (A) body mass and (B) wing length of chicks from Selvagem Grande in 2011 ($n = 4$) and 2012 ($n = 13$). Values are means \pm SD.

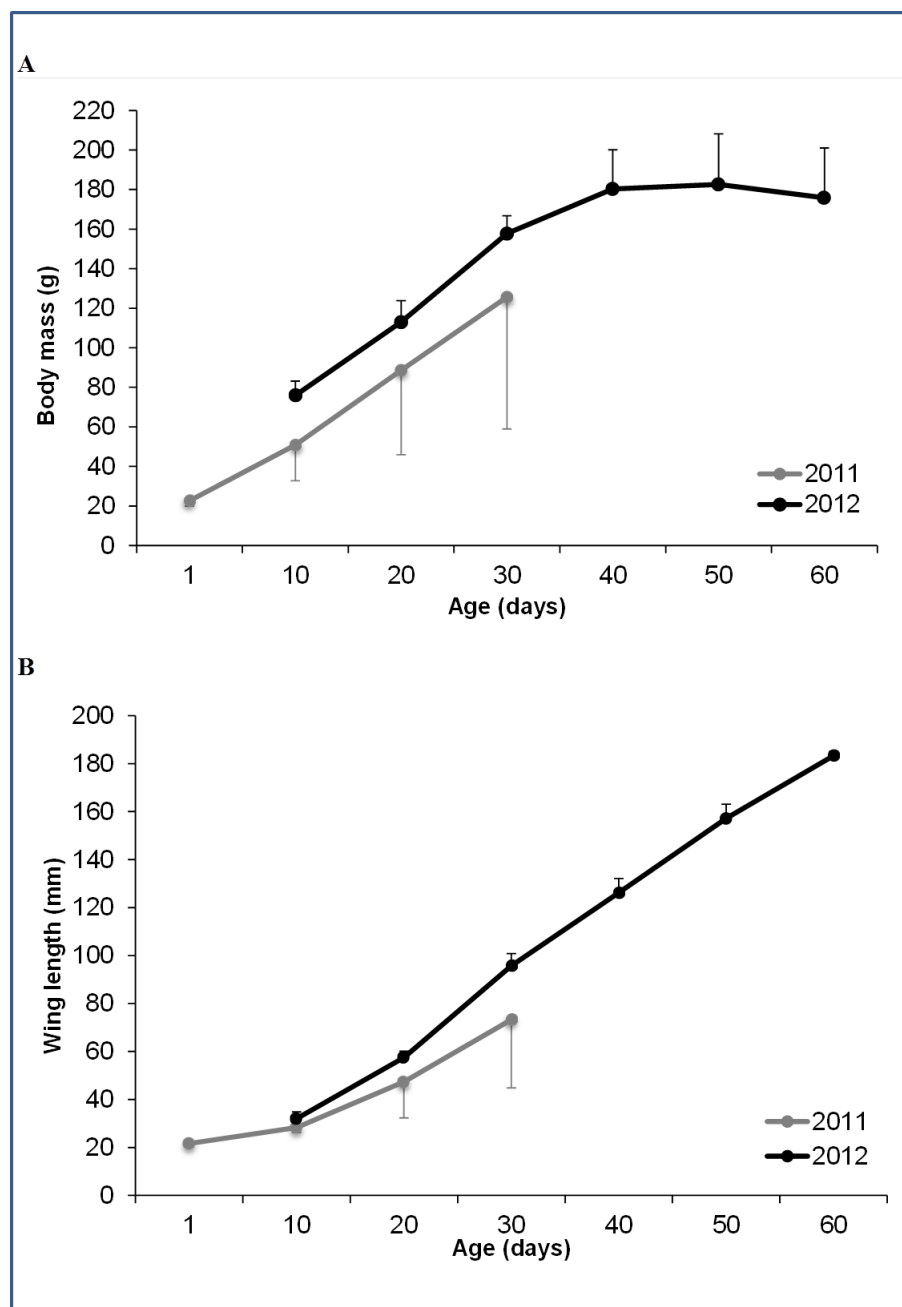


Table 1. Comparison of hatching and fledging success of Macaronesian shearwaters between Cima Islet and Selvagem Grande in 2011 and 2012, and causes of incubation failure and chick mortality.

| Year | | 2011 | | 2012 | |
|----------------------|-------------------|------------|-----------------|------------|-----------------|
| Island | | Cima Islet | Selvagem Grande | Cima Islet | Selvagem Grande |
| Nests (<i>n</i>) | | 13 | 15 | 10 | 26 |
| Hatching success (%) | | 61.5 | 33.3 | 90.0 | 65.4 |
| Fledging success (%) | | 62.5 | 80.0 | 66.7 | 64.7 |
| Egg failure (%) | | | | | |
| | Cracked | 38.5 | 20.0 | 0 | 19.2 |
| | Deserted | 0 | 46.7 | 0 | 0 |
| | Destroyed (storm) | 0 | 0 | 0 | 15.4 |
| Chick death (%) | | | | | |
| | Flooded (storm) | 0 | 0 | 0 | 11.7 |
| | Unknown causes | 37.5 | 20.0 | 0 | 23.6 |

Table 2. General linear models with binomial distribution, fitting the influence of nest characteristics on laying propensity and hatching success of the Macaronesian shearwaters from Cima Islet and Selvagem Grande. For nests where an egg was laid (1) or not laid (0) and nests where the chick hatched (1) or did not hatch (0), mean values \pm SD are given for each parameter. Substrate: soil, rock, or mixture of soil and rock. Orientation; north, east, south, or west. OR, odds ratio. Significant differences ($P < 0.05$) are printed in bold.

| | Cima Islet ($N = 26$) | | | | | | Selvagem Grande ($N = 62$) | | | | | |
|-----------------------------------|------------------------------------|-------------|--------------|-------------|--------------------------------------|--------------------------------------|------------------------------------|-------------|-------------------|-------------|----------------------------------|----------------------------------|
| Parameter | $\beta \pm$ SE | Z | P | OR | Laid ($N = 20$) | Not laid ($N = 6$) | $\beta \pm$ SE | Z | P | OR | Laid ($N = 39$) | Not laid ($N = 23$) |
| Intercept | 0.08 ± 0.78 | 0.77 | 0.20 | 0.45 | — | — | -4.27 ± 2.9 | 2.03 | 0.02 | 1.01 | — | — |
| Total depth (cm) | 4.61 ± 2.34 | 4.1 | 0.001 | 4.87 | 88.4 ± 9.3 | 64.0 ± 17.7 | 3.97 ± 0.16 | 3.62 | 0.01 | 1.43 | 70.8 ± 9.3 | 45.0 ± 8.3 |
| Chamber volume (cm ³) | -2.56 ± 1.97 | 2.18 | 0.01 | 2.19 | 3206.3 ± 909.1 | 8322.6 ± 761.0 | -1.46 ± 0.35 | 0.99 | 3.33 | 0.14 | 11521.4 ± 1627.5 | 8774.1 ± 1827.9 |
| Chamber depth (cm) | 0.56 ± 0.76 | 0.98 | 0.17 | 0.89 | 19.9 ± 9.8 | 19.8 ± 10.2 | 2.32 ± 0.55 | 1.69 | 0.09 | 0.98 | 25.4 ± 12.5 | 28.8 ± 7.3 |
| Substrate | 0.09 ± 1.92 | 0.34 | 0.24 | 0.24 | mixture | mixture | -8.16 ± 2.76 | 3.85 | 0.01 | 2.87 | soil | mixture |
| Orientation | 3.11 ± 2.98 | 2.08 | 0.02 | 2.01 | south | north | 9.37 ± 1.44 | 5.99 | < 0.001 | 4.32 | south | north |
| | Cima Islet ($N = 20$) | | | | | | Selvagem Grande ($N = 39$) | | | | | |
| Parameter | $\beta \pm$ SE | Z | P | OR | Hatched ($N = 15$) | Not hatched ($N = 5$) | $\beta \pm$ SE | Z | P | OR | Hatched ($N = 24$) | Not hatched ($N = 15$) |
| Intercept | 0.73 ± 0.15 | 0.56 | 0.53 | 0.63 | — | — | 0.89 ± 1.23 | 0.57 | 0.05 | 1.87 | — | — |

| | | | | | | | | | | | | |
|-----------------------------------|---------------------|-------------|--------------|-------------|------------------------|-------------------------|---------------------|-------------|-------------------|-------------|------------------------|-------------------------|
| Total depth (cm) | 1.01 ± 0.25 | 0.91 | 0.09 | 0.99 | 57.4 ± 2.6 | 49.6 ± 23.7 | 1.52 ± 0.73 | 3.01 | 0.10 | 0.65 | 86.7 ± 4.4 | 60.6 ± 2.9 |
| Chamber volume (cm ³) | -3.98 ± 1.76 | 4.26 | 0.001 | 2.90 | 6004.6 ± 1029.3 | 11770.8 ± 2637.2 | -4.98 ± 0.99 | 8.38 | < 0.001 | 1.91 | 6479.1 ± 1001.2 | 12339.8 ± 1908.5 |
| Chamber depth (cm) | 0.76 ± 1.90 | 0.92 | 0.12 | 0.88 | 17.9 ± 8.2 | 21.25 ± 10.8 | 2.54 ± 1.62 | 6.25 | 0.01 | 2.65 | 35.4 ± 8.4 | 19.7 ± 7.9 |
| Substrate | -3.10 ± 1.77 | 2.87 | 0.01 | 3.01 | soil | rock | -4.14 ± 2.19 | 8.26 | < 0.001 | 5.25 | soil | rock |
| Orientation | 1.09 ± 0.87 | 1.01 | 0.07 | 1.01 | west | West | 1.24 ± 0.52 | 2.18 | 0.23 | 0.67 | east | east |

Table 3. (A) Nest site fidelity expressed as the percentage of individuals which returned to the same nest in the Macaronesian shearwaters from Cima Islet and Selvagem Grande, and (B) occupation of Macaronesian shearwater nest sites by other cavity-nesting Procellariiformes during 2010–2013 (expressed as the proportion of nest sites occupied by other species).

| | | Cima Islet | Selvagem Grande |
|--|---------------------------------|-------------------|------------------------|
| (A) Nest site fidelity (%) | | | |
| | <i>N</i> | 11 | 33 |
| | 1 year | 91 | 78 |
| | 2 years | 9 | 18 |
| | 3 years | - | 3 |
| (B) Nest occupation by other seabirds (%) | | | |
| | <i>n</i> | 10 | 14 |
| | Cory's shearwater | 10 | 35.7 |
| | Bulwer's petrel | 70 | 64.3 |
| | Band-rumped storm petrel | 20 | 0 |